Journal of the Lepidopterists' Society
34(3), 1980, 286–294

SOME FACTORS RESPONSIBLE FOR IMBALANCES IN THE AUSTRALIAN FAUNA OF LEPIDOPTERA[1]

I. F. B. COMMON

Division of Entomology, CSIRO, Canberra, Australia

ABSTRACT. Major imbalances in the Australian fauna of Lepidoptera occur in families with high percentages of endemism, e.g., Tortricidae and Eucophoridae, which are associated with typically Australian plant communities and which have evolved especially with *Eucalyptus*. Events affecting the Australian environment from the Tertiary to present are discussed. Utilization of parts and stages of *Eucalyptus* by lepidopterous larvae is described. It is probable that similar selective factors were responsible for extraordinary species radiation in both Australian xerophytic plants and the insects dependent upon them.

The first Lepidoptera are believed to have evolved at least as early as the lower Cretaceous, and by the mid-Cretaceous forms similar to some of the more advanced Lepidoptera were already in existence (MacKay 1970). The greatest development of the Lepidoptera probably accompanied the proliferation of the angiosperms (Common, 1975) during the late Cretaceous epoch, and especially during the Tertiary. Nothing is known of the composition of the Australian lepidopterous fauna of the Tertiary, but it seems probable that it was very different from that of the present day.

The following greatly simplified sequence of events affecting the Australian environment from the Tertiary onwards (Galloway & Kemp, 1979) must have fundamentally influenced the composition and distribution of the Australian flora, and also the composition and distribution of the present-day fauna of Lepidoptera and other insects. From the lower Tertiary to the mid-Miocene the Australian continent was extremely flat, with uniformly poor soils and a relatively uniform moist, warm climate. A mesophytic flora was widespread, including various rain-forest genera such as *Nothofagus,* and typically Australian genera such as *Eucalyptus, Casuarina, Acacia,* and present-day genera of Proteaceae and grasses. Some mountain building occurred in the late Miocene and Pliocene, especially towards the eastern coast, culminating in the Kosciusko uplift, followed by extensive weathering and dissection in the eastern highlands. Marked fluctuations in climate were a feature of the Pliocene, with alternating periods of relatively dry and relatively moist conditions. Rapid changes in climate continued into the Pleistocene, associated with the formation and melting of Antarctic ice. However, glaciation was restrict-

[1] This paper is based on Dr. Common's Presidential Address, delivered at the Annual Meeting of the Lepidopterists' Society in Fairbanks, Alaska in June 1979.

ed to Tasmania and the Kosciusko area. Fluctuations in sea level through a range of some 200 m during this period produced intermittent land connections between the Australian continent and New Guinea in the north and Tasmania in the south. Intermittent favorable corridors connecting the south-east and the south-west of the continent were also created, as well as latitudinal shifts in climatic zones. The establishment of extensive dune systems before the end of the Pleistocene must have also represented significant biological barriers.

Progressive aridity from the late Miocene onwards favored the establishment of a xerophytic vegetation over much of the continent. The major pressures which were imposed on the widespread mesophytic flora of the early Tertiary resulted in the gradual retraction of the less adapted species to refuges along watercourses and in the moister areas of the east and south-east. Fluctuating climatic conditions, and innumerable modifications to the physical nature of the environment, including minor lava flows, weathering, dissection and the deposition of shales, sandstone, limestones, and alluvial soils, led to great habitat diversity. The successive retractions, expansions and migrations of the flora, and the associated fragmentation of populations and isolation of species, resulted in extensive species divergence and evolutionary radiation, and the gradual production of the diverse relatively xerophytic plant communities which occupy so much of Australia today.

Australia is still a relatively flat continent, rising to a maximum altitude of only 2100 m in the south-east. The soils on the whole are poor. An area equal to about one-third of the continent, reaching the coast near the tropic in the west and the Great Australian Bight in the south, has a rainfall of less than 25 cm annually. Beyond this area the rainfall increases in more or less concentric belts towards the coast, but two-thirds of the continent can be classified as semi-arid or arid, and much of the remainder is subject to long dry periods. In contrast, a small area of north-eastern Queensland has a rainfall of 400 cm annually, and the western coast of Tasmania more than 200 cm. The north of the continent receives mainly summer rains, whereas the south receives mainly winter rains.

Very broadly the present-day vegetation of Australia can be divided into the following major categories. In the north-east and in small pockets along the eastern coast, mainly in areas with a rainfall in excess of 150 cm annually, rain forest occurs, tropical in the north, subtropical in southern Queensland and New South Wales. In addition there are patches of temperate rain forest in Victoria and western Tasmania, and fragments of monsoon or gallery forest in northwestern Australia and the Northern Territory. Floristically the northern rain forests have much in common with those of south-east Asia. Elsewhere in Australia where the rainfall exceeds 37.5 cm annually, there are extensive areas of sclerophyll forests and savannah woodlands, with *Eucalyptus* species as dominants. Eucalypts do not occur in rain forest and the few that are found in the arid zone are distributed along watercourses or in special habitats. In the south, mainly in the 25–37.5 cm winter rainfall belt, mallee eucalypt communities are frequently developed. The arid zone of less than 25 cm rainfall annually supports various xerophytic plant communities, including extensive scrubs dominated by mulga and other species of *Acacia,* and grasslands containing native grasses and other herbs, but especially porcupine grass (*Triodia*).

The Lepidoptera of the Australian rain forests have been derived mainly from the Oriental and Papuan areas, and share many genera and species with south-east Asia and New Guinea. The characteristic Australian elements in the fauna are found in the sclerophyll and arid plant communities and no doubt have been evolved along with them. The two plant genera most frequently utilized as food by Australian Lepidoptera are *Eucalyptus* (Myrtaceae) and *Acacia* (Mimosaceae), but other genera of Myrtaceae and members of such typically Australian families as Proteaceae, Casuarinaceae and Epacridaceae (to name only a few) are frequently used. It is interesting to observe that of the 380 known species of butterflies only four polyphagous species of Lycaenidae have been recorded feeding on *Eucalyptus,* and relatively few feed on other typically Australian plant genera.

To the casual visitor, and indeed to many Australians, the sclerophyll forests appear to be monotonously uniform, dominated as they are by *Eucalyptus,* often with an understory of shrubs featuring *Acacia,* Proteaceae, Fabaceae, Myrtaceae and Epacridaceae. There certainly is a similarity about them, but to the more discerning observer they are far from uniform. There are at least 600 species of *Eucalyptus* and some 600 species of *Acacia* in Australia. In any restricted area the distribution of the dominant eucalypt species is controlled by such factors as soil moisture and soil nutrients, and slight changes in the microhabitat produce changes in the *Eucalyptus* dominants (Pryor, 1959). Each community usually has two, but sometimes up to six, co-dominant eucalypt species growing in stable associations.

Eucalypts range in size from dwarfs only a meter or two in height to forest giants. Most species are xerophytic and grow in localities where there is a marked shortage of water for a major part of the year, either as a summer drought in the winter rainfall areas of the south, or as a winter and spring drought in the north where the rainfall is largely confined to the summer months. Most are also resistant to fire and a few are tolerant of sub-zero temperatures at the treeline in southeastern Australia. Resistance to drought and fire is favored by the exceptionally thick bark of most species, and the development of a lignotuber, a swelling of the trunk at or just below ground level from which dormant buds can produce new shoots after the above ground parts of the tree have been destroyed. A mallee is a form of dwarf eucalypt which has a very large lignotuber below ground level and, instead of a single trunk, the lignotuber produces several branches which appear as a group of small slender trees. There are many species of mallee. Although three or four species of *Eucalyptus* occur in areas north of Australia, including New Guinea and Indonesia, the genus is believed to have originated in Australia.

The genus *Eucalyptus* is attacked by a wide range of Lepidoptera and other insects, and compared with eucalypts planted in many other parts of the world those which grow naturally in Australia are frequently retarded in growth by insect attack. Recurring severe insect defoliation sometimes kills the trees. Larvae of Cossidae, Hepialidae and Xyloryctidae bore in the trunk, bark and roots of eucalypts. Many species in other families mine in or devour the leaves, and a few feed on the flowers or woody seed capsules. Some of the foliage feeders restrict their attention to the young terminal growth, others to the mature leaves, and still others confine their feeding to the juvenile leaves (those leaves produced by the young eucalypt plant which may differ so much from the mature leaves in form and color that they might appear to belong to a different species). Families that include substantial numbers of species dependent on living *Eucalyptus* trees are the Hepialidae, Incurvariidae, Nepticulidae, Cossidae, Oecophoridae, Gelechiidae, Geometridae, Lasiocampidae, Anthelidae and Notodontidae. A few species in other families also feed on *Eucalyptus*, but it is interesting to note that several families such as the Phyllocnistidae, Epermeniidae, Pyralidae, Pterophoridae, Noctuidae and Agaristidae, as well as nearly all butterflies, avoid *Eucalyptus* entirely or almost so.

This great dependence of Australian Lepidoptera and other insects on *Eucalyptus* is remarkable when it is realized that eucalypt foliage contains substantial amounts of essential oils (Penfold & Willis, 1961) and phenols, including tannins (Hillis, 1966; Fox & Macauley, 1977). Several workers in the Northern Hemisphere have shown that insects tend to avoid foliage with a substantial phenol content, but many Australian insects appear to have evolved a high degree of tolerance to these substances. For example, Fox & Macauley (1977) showed that *Paropsis* (Coleoptera) larvae ingested and grew normally on a diet of young eucalypt leaves containing more than 25% dry weight of phenolic compounds, all of which passed through the gut unchanged and were recovered in the feces. They also showed that even young eucalypt leaves are extremely deficient in nitrogen, with levels ranging from 0.49% to 1.85%, compared with about 5% for young oak leaves. It seems clear therefore that many Australian insects, unlike their counterparts in the Northern Hemisphere, have become adapted to foodplants high in essential oils and phenols, and exceptionally low in nitrogen. Conversely, there are few if any of the introduced exotic insects in Australia that attack eucalypts or other typically Australian plants.

In addition to those species that feed on the living eucalypt tree, there are a great number that have adapted to feeding on fallen eucalypt leaves. Apart from such families as Tineidae and Blastobasidae, in which the larvae are frequently scavengers or detritus feeders, the larvae that depend on dead *Eucalyptus* leaves belong mainly to the Tortricidae and the Oecophoridae, but a few are found in the Gelechiidae, Xyloryctidae, Stathmopodidae, and Epipaschiinae (Pyralidae), and even in the Sterrhinae (Geometridae) and Hypeninae (Noctuidae). Some members of the Lecithoceridae are known to feed on dead eucalypt leaves and it is probable that the entire family is dependent on leaf litter. In recent studies on the composition of the leaf litter fauna in Australia a mean of 439 lepidopterous larvae per m^2 was reported (Plowman, 1979) from the litter in a wet sclerophyll eucalypt forest near Brisbane, and 99.8 larvae per m^2 in a mixed *Nothofagus-Eucalyptus* forest in Tasmania (Howard, 1975).

Large sections of the Australian Tortricidae and Oecophoridae have apparently co-evolved (Ehrlich & Raven, 1965) with the typically Australian plant communities, especially with the eucalypts. For the purposes of this discussion the family Oecophoridae is used in the sense of Common (1970). This is by far the largest Australian family of moths and includes more than 2000 named species and a further 1500 known species that are not yet described; it has an estimated total of 5500 Australian species. The named species have been referred to more than 290 nominal genera which, with synonymy, can be reduced to a maximum of 240 genera; with further revision there may prove to be less than 200 named genera. Most of these are endemic and many additional endemic genera await description. Only a few, mainly rainforest genera, are shared with New Guinea and south-east Asia and, in the present state of our knowledge, there appear to be few near relationships of the Australian fauna with that of New Zealand, South America or South Africa. The origin of the ancestral Australian Oecophoridae is unknown, but it seems clear that the extraordinary evolutionary radiation of this group occurred within Australia itself and

TABLE 1. Australian Oecophoridae and Tortricidae reared from *Eucalyptus*.

		Number & percent of species on *Eucalyptus*					
	Total reared	Living leaves		Dead leaves		All leaves	
TORTRICIDAE							
Total	199	13	(7%)	40	(20%)	53	(27%)
Tortricinae	141	9	(6%)	40	(28%)	49	(35%)
Olethreutinae	58	4	(7%)	—	—	4	(7%)
OECOPHORIDAE							
Total	322	79	(25%)	188	(61%)	267	(83%)
Depressariinae	16	3	(19%)	—	—	3	(19%)
Other subfamilies	306	76	(25%)	188	(61%)	264	(86%)

presumably paralleled the radiation in the characteristic Australian flora.

The Australian Tortricidae include 600 named species and a further 300 known species not yet described; a total of 1200 Australian species has been estimated for the family. Unlike the situation in most other regions, the Tortricinae outnumber the Olethreutinae. The number of Olethreutinae is probably comparable with that of other major areas of similar size, but well over 500 Australian Tortricinae are already known, of which only 360 are named, and the total is estimated at nearly 700. The difference in magnitude between the Australian representation of this subfamily and that in other regions may well be related to the adaptation of many Australian genera to the xerophytic sclerophyll plant communities, especially to *Eucalyptus*.

Of the 322 species of Australian Oecophoridae that have been reared, 79 (25%) are restricted to green *Eucalyptus* leaves, and 188 (61%) are dependent on dead eucalypt leaves (Table 1). Few, if any, of the dead leaf feeders belong to the Depressariinae, a group represented in Australia by only 21 named genera, nine of which appear to be restricted to rain forest. If the 322 oecophorid life histories constitute a representative sample of the family in Australia, we could expect to find a total of 4000 species dependent on *Eucalyptus*, and three-quarters of these dependent on dead eucalypt leaves.

Of the 200 species of Australian Tortricidae that have been reared, only 4 (7%) of the 58 Olethreutinae are restricted to living *Eucalyptus* foliage and 9 (6%) of the 141 Tortricinae. Whereas none of the reared Olethreutinae are known to feed on dead eucalypt leaves, 40 (28%) of the reared Tortricinae do so. In this respect the Australian Tortricinae are unique.

This remarkable development of dead-leaf feeding in the Australian Oecophoridae and Tortricidae may well be an adaptation to the physiological processes responsible for leaf-shedding in *Eucalyptus.* The length of time eucalypt leaves remain on the tree is surprisingly short for evergreen species and has been estimated to average no more than 18 months. However, the life of leaves is extremely variable depending on the species and the position of the leaves on the tree, and leaf-fall can be initiated by flowering or fruiting, by periodical bursts of growth in the tree, by insect attack, and by fire. After insect attack leaves are renewed from accessory buds and the older insect-damaged leaves are shed. At all seasons of the year eucalypts shed leaves, especially the mature leaves (Jacobs, 1955; Penfold & Willis, 1961). Here then, in the evolving eucalypt-dominated sclerophyll forests and woodlands, an abundant supply of leaf litter food, probably with a high phenol and a very low nitrogen content, awaited any organisms which had the genetic potential to occupy such a niche, a challenge that was squarely met by many Oecophoridae and Tortricinae.

In the Oecophoridae most of the species that feed on living *Eucalyptus* leaves utilize the mature foliage. It follows, therefore, that should the mature leaves harboring larvae be shed before the larvae have reached maturity, survival may well depend on the ability of each species to utilize wilting, partially dry or even completely dry foliage on the ground. Although the capacity to feed on fallen foliage has probably evolved many times in the Lepidoptera, it seems probable that in many of the Oecorphoridae, this was the mechanism which resulted in such a behavior pattern. In the genus *Ocystola,* for example, the larvae of some species feed on green *Eucalyptus* leaves, joining adjacent mature leaves in a characteristic fashion to produce a roomy cell in which the larva forms a flattened elliptical case of silk and fecal pellets. Feeding takes place within the cell on the surface tissue of the two leaves and pupation occurs in the enclosed case. In other closely related species of *Ocystola,* similarly joined recently dead leaves, with the larval case between, are commonly found on the ground beneath the eucalypts from which the leaves have been shed. Such larvae can continue to feed on the drying leaf tissue and emerge successfully as adults. The larvae of some other species of *Ocystola* feed throughout life on dead leaf litter. Other genera, or groups of closely related genera, provide similar examples.

One might suppose that leaf litter would provide a very uniform habitat, with little opportunity for the development of special adaptations and the application of selective pressures. However, in a semi-arid environment this is far from the truth, and the Australian Oecophoridae have developed many novel devices for survival. Desiccation and extremes of temperature must seem almost insuperable barriers in the relatively harsh Australian environment, but the Oecophoridae have overcome these problems by constructing a wide range of larval cases or larval shelters, or other means to avoid or resist such hazards. In the genus *Garrha*, for example, the larvae live in portable lenticular cases usually found under leaf litter and feed at night. In situations in which the leaf litter is sparse and the diurnal temperatures are high, the larvae of some species attach the case with a few strands of silk vertically to a grass stem so that it is a few millimeters clear of the hot ground and the narrow edge of the case is oriented towards the sun, thus reducing the effects of radiant and conducted heat. The larvae of some species of oecophorids are also able to resist or avoid the effects of fire to some extent, their populations being restricted during hot and dry weather to slightly moist places beside the butts of trees, beside or under logs or stones, or in hollows in the ground or in dead stumps, or even under loose bark on tree trunks. And as long as the areas burnt are not too extensive, or as long as unburnt islands remain, some species can apparently respond to the abundant leaf-fall following the fire and rapidly re-establish in the burnt areas.

For long the life history of the litter-feeding Tortricinae was unknown, despite the fact that the adults of some are often very common. I first suspected that they may feed on green *Eucalyptus* leaves, perhaps high in the tree canopy where they may have been overlooked. After obtaining fertile egg masses from captured females, I offered the newly hatched larvae sandwiches of young freshly cut green eucalypt leaves. The young larvae quickly settled down in silken shelters between the leaves and fed readily. As the leaves deteriorated I carefully transferred the young larvae to fresh young leaves and in this way reared them successfully. However, I found that young larvae of the same species still continued to feed freely and reached maturity even if the original green leaves were not replaced, as long as they did not dry out completely. It seemed probable therefore that the larvae might be adapted to feeding on dead eucalypt leaves throughout life, and persistent search in the leaf litter subsequently yielded larvae of many species. As in the Oecophoridae, the larvae were not found to be generally distributed in the litter, but were restricted to microhabitats characteristic of each species. Hence, tortricine larvae occur amongst leaves which have accumulated in the hollowed-out tops of dead stumps, on logs, close to the butts of trees and stumps, amongst rocks, or behind loose bark on tree trunks. Some can be found most easily between joined dead leaves still adhering to recently fallen twigs and branches. At one stage I thought that such larvae may have been shed with the green leaves from the tree, but this does not appear to be so. Over the litter, I randomly distributed a series of freshly cut twigs of *Eucalyptus*, each bearing about a dozen leaves; I then examined these 24 hours later and found several nearly mature *Meritastis* larvae between joined leaves on these freshly cut twigs. The larvae of this and other species are evidently quite mobile in the litter and are attracted to the freshly fallen leaves as food.

Major imbalances in the Australian fauna of Lepidoptera occur in those families which have the highest percentage of endemism and which are associated with diverse and relatively xerophytic plant communities. It seems very probable that these insect groups evolved along with the typically Australian plant communities with which they occur, and that similar selective factors were responsible for an extraordinary species radiation in both the xerophytic plant hosts and the insects dependent upon them.

LITERATURE CITED

COMMON, I. F. B. 1970. Lepidoptera (Moths and butterflies). Pp. 765–866 *in* The Insects of Australia. Melbourne, Melbourne University Press. 1029 pp.

——— 1975. Evolution and classification of the Lepidoptera. Annu. Rev. Ent. 20: 183–203.

EHRLICH, P. R. & P. H. RAVEN. 1965. Butterflies and plants: a study in coevolution. Evolution 18: 586–608.

FOX, L. R. & B. J. MACAULEY. 1977. Insect grazing on *Eucalyptus* in response to variation in leaf tannins and nitrogen. Oecologia (Berl.) 29: 145–162.

GALLOWAY, R. W. & E. M. KEMP. 1981. Late Cainozoic environments in Australia. *In* Biological Ecology of Australia (ed. A. Keast), in press.

HILLIS, W. E. 1966. Polyphenols in the leaves of *Eucalyptus* L'Herit: a chemotaxonomic survey. I. Introduction and a study of the series Globulares. Phytochemistry 5: 1075–1090.

HOWARD, T. M. 1975. Litter fauna in *Nothofagus cunninghamii* forests. Proc. R. Soc. Vict. 87: 207–213.

JACOBS, M. R. 1955. Growth Habits of the Eucalypts. Canberra, Commonwealth Government Printer. 262 pp.

MACKAY, M. R. 1970. Lepidoptera in Cretaceous amber. Science 167: 379–380.

PENFOLD, A. R. & J. L. WILLIS. 1961. The Eucalypts. New York, Wiley Interscience Publishers. 550 pp.

PLOWMAN, K. P. 1979. Litter and soil fauna of two Australian subtropical forests. Aust. J. Ecol. 4: 87–104.

PRYOR, L. D. 1959. Species distribution and association in *Eucalyptus*. Pp. 461–471 *in* A. Keast et al., eds. Biogeography and Ecology in Australia. Den Haag, Junk. 640 pp.